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Church, Arthur Henry

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ELEMENTARY NOTES ON THE
REPRODUCTION OF ANGIOSPERMS

By

A. H. CHURCH, M.A.

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Reproduction: Apart from somatic organization of the leaf, stem, and root, constituting the working mechanism of the life of the *individual*, it is necessary to consider the mechanism for maintaining the existence of the *race*, as the individuals wear out, owing to the imperfection of metabolic mechanism, and die. The subject also includes:—

- (1) The possibility of the improvement of the race, as progression in *time*.
- (2) Dispersal to new stations, as progression in *space*.

Dispersal implies enormous *Wastage*, in the chance of finding new stations, and further wastage in competition for unoccupied ground, with individuals of the same race, or different forms of organism. Beyond the maintenance of its own existence and growth, the entire working life of the organism may be spent in compensating wastage. If this is not done the race dies out. Races exist on the 'Law of the Minimum'; so that output of reproductive units of different categories may be taken as the price of existence (*Wastage-coefficient*). Hence reproduction includes the production of a multitude of individuals as a secondary feature; but mere multiplication can be effected quite as efficiently by '*Vegetative Propagation*'. Economy in such wastage is the criterion of higher organism; the mechanism of reproduction of the Flowering-plant being so far the highest expression of successful plant-organism.

Angiosperms: In Flowering Plants of higher order the whole of the reproductive processes are included within the mechanism of special shoots distinguished as *Flowers*, attaining their limit in the production of seeds, from which individuals of type similar to the parent organism can be produced, as a fact of general experience. The organization of the flower includes a series of extremely complex phenomena, only to be understood by tracing its evolutionary progression from earlier stages of plant-life. The analysis of the mechanism of flowers is the most important part of Botany from the standpoint of Reproduction, rather than from that of Systematy; the latter follows as a consequence.

Ancient History: Vague ideas of 'sex' in plants go back to remote epochs (cf. Date-Palm). Linnaeus (XVIII century) regarded a flower as a sexual mechanism; stamens male, and 'pistils' female; hence such terms as *ovary*, *hermaphrodite*, etc., are still retained in metaphorical sense as convenient conventions. Phenomena analogous with *sex* in animals are microscopic in dimensions, and wholly enclosed in the tissues; the reproductive mechanism is more complex, and in many respects more advanced, than in any animal.

General Idea of a Flower. A shoot-system, with characters different from the normal photosynthetic shoot, set apart to perform the whole of the reproductive functions, sexual and asexual, culminating in the liberation of seeds, and including the essential mechanism of:—

- (1) Pollination, (2) Fertilization, (3) Dispersal,

as also the developmental history of:—

- (1) Spores, (2) Gametes, (3) The Embryo, respectively,

and the mode of nutrition of these respective units.

Definition: 'An axis bearing sporophylls'; with emendations;—

- (1) A special axis, i. e. a branch (= strobilus).
- (2) Sporophylls, as spore-producing leaf-members, bearing spores of 2 kinds, Micro- and Mega-, as the 'hermaphrodite' condition.
- (3) With accessory protective members (perianth), and arrangement in definite sequence (= anthostrobilus).
- (4) The parts co-ordinated by growth-factors, and time-factors, to constitute a floral mechanism; the first object of which is to secure *cross-pollination*, i. e. pollinated from another individual of the same species.

Parts of a typical Flower, as an average modern limiting form:—

- (1) A bud-formation, producing leaf-like members; without much intercalary extension in the axis, conveniently termed the *Receptacle*.
- (2) Either sessile, or extended on an internodal growth as 'flower-stalk' (*peduncle*).
- (3) Outer floral leaves, accessory and protective, as *Perianth*.
- (4) The essential organs of Sporophylls, as:—

(a) Stamens, collectively termed the **Androecium** :

(β) Carpels, collectively constituting the **Gynoecium** ; as special regions of the floral system.

In higher floral types, some of the original androecial members are adapted as coloured laminae (petals of the corolla), and the outer perianth-members are then distinguished as the **sepals** of the calyx.

The corolla-petals are normally 'coloured' (other than green); as the sepals are normally green, but not invariably so; the coloured condition may be distinguished as 'petaloid', in calyx or perianth.

Symmetry of the construction, primarily centric (Radial, Regular, Actinomorphic); in specialized types eccentric (Irregular, Dorsiventral, Zygomorphic). In extreme cases such zygomorphic flowers are orientated with the vertical, geotropically, in correlation with visitation by similarly orientated insects, as Bees.

Arrangement of Parts follows phyllotaxis-patterns; spiral or more commonly whorled, giving precise mechanisms; but complex, and combinations of spiral and whorled in same flower; low numbers 2, 3, 5 prevail (4 and 6 as variants on 5): cf. dimery, trimery, pentamery, &c.

Secondary Complications with wide range: as by secondary growth-zones (intercalary extensions) affecting groups of members:—

(a) cf. gamophylly, gamosepaly, gamopetaly, staminal tube, syncarpy:

(β) or individual members; cf. petal 'claws', stamen 'filaments', style:

(γ) Special case of complex ovary-formations, with types of 'placentation'.

Normal acropetal production of members on an abbreviated conoidal receptacle gives the case of *Hypogyny*, and the 'Superior ovary' of older writers.

A hollowed or crateriform apex may drop the terminal gynoecium below the level of the outer members (*Perigyny*): the ovary-cavity may be involved in later extension as a state of *Epigyny*, with 'Inferior ovary'.

Colour-effects, due to residual pigments of the chlorophyll-apparatus acquiring new functions, as attraction of insects; mainly due to:—

(a) *Carotin*, yellows and reds, pigment in plastids (Carrot, Buttercup).

(β) *Anthocyan*, purple-reds, violet, and blue, soluble in cell-sap (cf. Beetroot, Copper-Beech).

(γ) White flowers by total elimination of all pigments, and air-films in tissues.

A colour-contrast is more generally aimed at, rather than any special tint.

Reduction-effects: Whether due to decadence or specialization, imply loss of parts: e.g. aphyllly, apetaly, dicliny (monoecious, dioecious), 'neuter' flowers. The limiting case of a flower may be a staminate flower reduced to one stamen: or a carpellary flower reduced to one carpel; or two carpels, syncarpous, including one ovule.

Time factors: involving co-ordination of growth-rates and movements in different parts of the mechanism: Sequence of Events; Bud-expansion; Final adjustments; Closing-movements; Proterandry, protogyny; Daily period; Shedding of parts by abscission.

Tabulation and schedule of Form-Factors.

(1) *Floral formula*, meagre method, in various types and symbols, e.g.:

S, 5; P, 5; A, 5+5; G ($\bar{5}$).

(2) *Floral diagram*, as conventional ground-plan; useful for whorled flowers with few parts; based on bud-sections:

Orientation, on 2 axes at right angles, with Median (Antero-Posterior) plane, Transverse plane, Diagonal planes: the subtending bract (anterior); the parent axis (posterior); prophylls (lateral).

Representation of parts: conventionalized transverse sections of leaf-members (sepals and petals); of anthers, in androecium; and transv. sect. of ovary (low power), for gynoecium.

Accessory details as nectary-glands; prefloration, quincuncial, valvate, convolute; stigmas, spurs, bilaterality and plane of zygomorphy.

(3) *Sectional Elevation*, as scale-drawing of half the mechanism, and cut in given direction; commonly in median plane (P to A), and constructed in all detail to scale (e.g. $\times 10$): finished figure in accurate colour-scheme: similar constructions for different phases of complex mechanism.

ANDROECIUM, of Stamens, usually few, 5-10 (range 1-1000), devoted to the production of pollen-grains or *microspores*: hence the stamen is regarded as equivalent to a leaf (*microsporophyll*), with a petiole (filament), and lamina, rudimentary as 'connective', bearing 4 sporangia in 2 pairs along the margin of the lamina, as two sori each of two sporangia; a limiting case, hence remarkably constant for the vast majority of flowers. Anthers with two sporangia are exceptional.

The sporangia are termed 'pollen-sacs', and the whole set of 4 constitutes the anther (4-lobed); a single V.B. in filament and connective supplies the anther. The sporangia dehisce in pairs, by a special mechanism, and the pollen-grains are liberated in the air.

Note theoretical names, and older more colloquial terms as equivalents.

Development of Pollen: the young anther-lobes consist of simple parenchymatous units, and at an early stage, cells are differentiated in each lobe as an *Archesporium*, distinguished by refractive or denser plasmatic contents with conspicuous nuclei. At first covered by only a single layer of epidermal cells, by active division the archesporial units produce a central mass of 'mother-cells'; while an outer tract subdivides to wall-layers, 2-3 cells thick, as the lobes of the anther enlarge. The mother-cells tend to isolate, and round off, presenting remarkable phenomena in nuclear division, the importance of which does not immediately appear, as:—

Meiosis: In each mother-cell, after elaborate preparatory changes (to diakinesis), a nuclear spindle is formed; the chromosomes are distributed in pairs over the equatorial plate, but longitudinal division of each chromosome is checked. Spindle-fibres attach instead to the individual chromosomes still imperfectly divided, with the result that half the number are withdrawn to each pole (anaphase), there to recombine to constitute the daughter nuclei (telophase), each with only half the regulation number, since whole chromosomes are sorted out and not halves. Hence termed a 'Reduction Division'. The daughter nuclei divide again directly with a spindle-mechanism, the chromosomes now completing their longitudinal fission; but the resulting nuclei continue to present the half-number (hence termed '*haploid*', as distinguished from the full somatic or diploid type). The division of the mother-cells in this manner marks a critical departure in the life-history, and the 4 resultant nuclei produced in each, which are not necessarily at first separated by new dividing walls, may be termed a *tetrad-group*. These nuclei segregate cytoplasm, round-off, and secrete wall-membranes, soon becoming isolated as the young pollen-grains. In this way pollen-grains are developed in groups of four, and the tetrad-formation may persist until they are mature; in some cases they remain so associated.

Nutrition of Pollen-grains: A zone of cells around the mass of mother-cells early differentiates as a feeding-layer, with refringent contents and active nuclei, in the manner of the epithelium lining a duct, as the *Tapetum*. Food-supplies are secreted into the cavity of the 'pollen-sac', and the pollen-grains grow to pack the space, being fed from without. When the latter are fully grown only a trace of the tapetal layer persists, with no cell-structure. Oily colouring matters derived from the tapetum commonly tint the pollen-grains yellow, brown, orange-red, or even blue.

Pollen-grains when fully formed appear as uninucleated cells, commonly 30-50 μ diam. (10-100), spherical, or more or less tetrahedrally angular, with reserve-contents as oil-drops and proteids, and a double wall, or *exine* of cuticularized layers covering an *intine* of cellulose. Thin areas in the former, or in both layers, constitute *pores*, often definite in number and position; very commonly 3 at 3 angles. Sculpturing of the outer wall, spinous projections, etc., may give characteristic appearances to specific or generic types. Tetrad-groups may persist (*Erica*), or packets of more (*Acacia*); in extreme cases (Orchids) the entire contents of each pollen-sac may remain united in a waxy cake-like mass as a *Pollinium*. Exposed to the air, pollen-grains dry off, becoming shrunken and folded, and are normally airborne by wind, or carried by hairy insects: very rarely (some aquatics, *Zostera*) discharged under water.

Dehiscence of Anther. Two pollen-sacs on either side open by one line of separation, in response to hydrostatic tensions in the living cells of the outer wall-layers as these tend to lose water. Sub-epidermal layers show a thickening of bands or reticulated strands, which may be lignified, these being so arranged as a supporting

framework to the cells, that as the latter lose water, the walls tend to curve in the opposite sense, and thus exert a tension on the dehiscence-line. Anthers in which this mechanism is imperfect or immature do not dehisce. The pollen is normally exposed passively on the recurved wall-portions.

Germination of Pollen: Supplied with fluid and sugar in solution, as on the stigmatic region of the flower, *pollen-tubes* are projected from one or more pores, these extending as delicate processes, much in the manner of root-hairs, becoming parasitic on the tissue of the style. The deposition of pollen-grains on the stigmatic surface constitutes the act of *Pollination*: germination to a new individual normally follows. *Note* that the pollen-grain is a simple 'asexual' unit; it germinates directly without reference to any other cell-unit (i. e. it is not 'male').

Pollinating Agents. The oldest agency for the translocation of pollen is that of the wind (Anemophily). Pollination by Insect-agency (Entomophily) implies correlation with animal organism, restricting the wastage of the former process. Insects of lower grade (flies) may take pollen as food; bees collect pollen for larvae, taking sweet secretion of nectary-glands for themselves: Lepidoptera take 'honey' only, as also do Humming-birds: precision of visitation, speed in working, increase chances of *cross-fertilization* and further economize pollen-output, as expression of higher organization. In all cases autogamy, the transfer of pollen produced by the same flower or the same individual, is to be avoided, and much floral mechanism is devoted to this end. Persistent autogamy implies deterioration of the mechanism and decadence, with ultimate stage in cleistogamy, in which case the flowers fail to open. The 'opening' and presentation of a floral mechanism implies that a chance is given to cross-pollination with its consequences in the production of cross-fertilized seeds.

Mechanism of Presentation. Pollen is exposed to the influence of the wind, or put in the way of insect-visitors by the filaments, as expressed in:—

(1) intercalary extension, (2) growth-curvatures as effects of geotropic response, (3) special movements of divergence or erection, collectively or individually, (4) often correlated with a reversed action after the presentation period.

The dehiscence of the anthers may also bear a special relation to the growth-period of other floral organs; e.g., when the anthers dehisce before the stigma is receptive the mechanism is *proterandrous*; the converse condition being *prologyny*, as tending to eliminate autogamy.

Staminate flowers produce functional stamens only, the gynoecium being reduced and functionless, vestigial, or wholly wanting. The same applies to the androecium of 'carpellary flowers'. Staminate flowers are only 'male' to the extent that the pollen-grains germinate to give only male individuals in the life-cycle. Germination of the pollen-grain commonly begins before the grains are shed from the anthers; in which case two nuclei may be distinguished in the cytoplasm.

Microscopic Examination.

Large stamens of *Fritillaria imperialis* show generalized construction. Cut in transv. sect.; anthers 3 mm. broad, 4-locular, with walls of loculi of banded cells 2-3 deep; aqueous epidermis with finely granulated cuticle, 75 μ diam.; hypodermal banded cells, 150 μ deep, with protoplasmic contents and nuclei, the wall with reticulated thickening strands. In these large ill-differentiated anthers the banded cells extend over walls and connective region. Pollen-grains, oval, 50 μ , may show 2 nuclei.

Buds, half-grown, of *Helleborus foetidus* (10 mm. diam.) with numerous enclosed young anthers, are cut in transv. sect. of whole upper region, and sections of anthers (1½ mm. broad) sorted out.

Anthers 4-locular; dehiscence-layer at junction of 2 loculi on either side; V.B. in connective; pollen 30 μ ; wall differentiated only along the cavity of the pollen-sacs:—

- (1) Epidermis of aqueous cells (40 μ) with finely granulated cuticle.
- (2) A single hypodermal layer of banded cells, 40 μ deep, each with 2-3 thick bars (3 μ) and thickened inner wall, lignified in older stages.
- (3) Remains of tapetum lining the cavity, and slight expression of other parenchymatous layers of wall.

For Meiotic phenomena cf. buds of *Lilium Martagon*: Chromosome number 24, showing 12 bivalent chromosomes in the equatorial plate of the reduction spindle.

GYNOECIUM, similarly based on specialized leaves as *Carpels* or *Megaspophylls*. These bear megasporangia, commonly termed *Ovules*, in which one large spore is alone functional. Differentiation of an Ovary-chamber is the essential character of the Angiosperm, as special adaptation for the protection of the ovules from desiccation during their entire history to the stage of the Seed. Special cases may be distinguished, as:—

I. **Apocarpus** : The typical carpel may be regarded as a leaf-lamina bearing marginal ovules, and rarely with much of a stalk; the lamina being folded on its upper surface to give an ovary-cavity; the margins fused along a *suture*, and the tip elongated as *style*, with a more or less closed *stigma*, as receptive surface, at the extremity. Vascular supply to the ovules, originally one V.B. to each ovule; the ovules many or few, ultimately one only as limiting case, and commonly found.

The apocarpous gynoecium is the oldest and most elementary form of ovary-construction: cf. *Pea-Pod* (*Leguminosae*), *Aquilegia*, with many ovules; *Clematis* with one only functional; *Ranunculus*, one ovule only produced in each carpel.

II. **Syncarpus** : a more elaborate case, initiated by secondary growth-extension intercalated below the original carpel-primordia; the latter may be reduced, and soon become more or less vestigial, as the ovuliferous function is passed on to the new 'syncarpous' zone; remains of the original carpels may be traced in free styles or stigmas; or the carpels may leave no trace beyond numerical suggestions, and the stigmatic surfaces be of secondary nature; e.g. 'commisural', cf. *Wallflower*.

In the simplest case the intercalated chamber is unilocular, and the ovules are borne on the outer wall (case of 'parietal placentation'); the number of placentas expressing the original carpel-number.

A more complex case occurs commonly, giving 'axile-placentation', in which pocket-depressions below the level of the floral apex, may be specialized as ovuliferous regions; the component loculi again presenting all phases of reduction to few, or ultimately one ovule each.

Both cases may co-exist, in greater or less degree, with a wide range of possibilities, rendering generalizations under simple headings difficult, or even obscure; often characteristic for large groups as 'families' founded on such features.

III. **The Inferior Ovary** : Previous examples assume the case of an ordinary conical receptacle, as a 'condensed' shoot-system, implying an axis with terminal growing-point. The case of the crateriform apex involves further possibilities, as leading to more efficient protection and vascular supply of the ovary-chamber. In all cases development is traced by reference to the apex of the floral axis. In the inferior ovary the outer wall is receptacular in origin, and the ovuliferous region may present parietal or axile placentation, or again any phase of reduction in ovule-content. A limiting case of two carpels in a syncarpous construction may be associated with production of one basal ovule only (*Compositae*).

Note: the object of such construction is (1) the maximum protection of the ovules; (2) efficient vascular supply; (3) chance of cross-pollination independently; (4) greater possibilities of special adaptation in fruit-stages, as also in dispersal-mechanisms. Reduction-specialization in ovule-output, as controlling seed-output, is a mark of higher organization.

The Style includes any secondary intercalary extension of a carpel-tip, or distal end of ovary-region, utilized for the presentation of the surface specialized for the reception of pollen-grains, and distinguished as the *Stigma*; originally merely the point at the end of the carpellary leaf, as the last vestige of the open suture. This is extended to special cases, as a plumose tuft of ramuli giving increased area for collection of wind-borne pollen; or more extensive glandular regions, commonly papillose, and more or less damp or viscid, for the adhesion of insect-borne pollen, thus rubbed off on the brush-work of stigmatic papillae. The protection of such a damp surface of delicate cell-units may be an essential factor in special cases of floral mechanism, and any secretion must be regulated in osmotic value to that of the pollen-grains germinating on it; hence often a specific constant, and the chances of 'foreign pollen' germinating on any stigma may be remarkably small. The elongation of the style is commonly correlated with similar spacing-growth of stamen-filaments, or is utilized in the

elimination of autogamy. Special growth-curvatures and movements may be effected during the period of floral presentation.

The Ovule: Typically small and much like the egg of insects, as flies and moths, hence name; strictly a megasporangium producing one megaspore, as the limiting case. Originating as a massive emergence of the carpellary margin, or 'placenta' (*nucellus*), on a stalk-portion (*funicle*), not always expressed; and invested by 2 (or 1) collar-growths (*integuments*), outer and inner, closing over the apex of the nucellus leaving only a narrow pore (*micropyle*).

The body of the ovule is commonly bent on the stalk (*raphe*) in anatropous fashion; bent on itself (campylotropous) or more rarely orthotropous. Nutrition is effected by one V.B. terminating in the chalazal-region. Within the nucellus one large megaspore is differentiated; stages of archesporium, tetrads, tapetum, etc., are abbreviated as vestigial relics, but meiosis occurs, and the surviving spore is one of a tetrad: it is commonly known as 'embryo-sac' (megaspore).

The special point is that this spore is not shed but germinates *in situ* directly, the 'spore-stage' being imperceptible: this expresses the state of the Phanerogam or Seed-Plant, as the necessity for a dispersal-stage (*seed*) follows at some later date from such failure of the original mechanism of spore-discharge.

Note the function of the carpel is to produce ovules each with one megaspore: that of the stamens to produce pollen-grains: the latter, in pollination, are brought *as near as possible* to the vicinity of the megaspores, that they may germinate and grow to new individuals, side by side: Both types of spore give rise to minute holoparasitic structures as the sexual phases of the organism.

NARCISSUS *poeticus* affords a convenient type, the female prothallus being ready for fertilization when the flowers are at their best. In many types with large ovaries (*Lilium*, *Tulipa*, *Iris*) this does not obtain.

Gynoeceium, syncarpous, of 3 carpels, ovary inferior, placentation axile; ovules numerous and fairly transversely extended in the loculi. The flower is horizontally projected, with white star-perianth, target-eye, powerful scent, and narrow tube (30 mm.) to honey-supply from septal-glands of ovary opening at base of style, as a highly specialized Moth-mechanism.

Transv. sect. of ovary, material fixed in abs. alc., gives good results:

Note: large ovules, oval, 1 mm. broad; micropyle, integuments, the outer one fused with raphe along one side; V.B. prominent in raphe, and defining the chalazal region. *Embryo-sac*, as large oval cavity, empty, or with scanty contents, 450–500 μ long.

Contents of Embryo sac, not necessarily seen in same section, as a few large nuclei, and strands or portions of network of plasmatic bridges.

(1) **Micropylar group** of three nuclei; as oosphere, 50 μ diam., a large nucleus with film of cytoplasm only: two smaller synergidae, 20 μ nuclei, with slight cytoplasm.

(2) **Central fusion-nucleus**, large 60 μ diam., spherical, aqueous, with conspicuous nucleolus; often out of position, and resting on antipodal group.

(3) **Antipodal group** of 3 nuclei, 30 μ or more, with nucleoli, surrounded by vacuolated cytoplasm and thin cell-walls; in a close cluster.

The whole constitutes the female prothallus as a distinct individual organism, in no protoplasmic continuity with the nucellus, and wholly parasitic on it, as a minimum organization, the culmination of a long line of descent from a prothallus bearing archegonia in the manner of a *Fern-prothallus*, and beyond this from a free-living algal organism of aquatic submerged habit. As types of gynoeceium cf.:—

Wallflower: Tetramerous, actinomorphic; Gynoeceium based on 2 carpels; ovary syncarpous, superior, 2-locular, with parietal placentation and numerous ovules: stigma 2-lobed, commissural.

Viola: Pentamerous, zygomorphic; Gynoeceium based on 3 carpels; ovary syncarpous, superior, unilocular, with parietal placentation, numerous ovules. Style bent, stigma papillose, not lobed.

Clematis: Tetramerous (5–6), actinomorphic, coloured perianth only; Gynoeceium apocarpous of indefinite carpels, each with one anatropous suspended ovule and rudiments of others.

Snapdragon: Zygomorphic, gamopetalous, 2:3-lipped corolla: Gynoeceium based on 2 carpels; ovary syncarpous, 2-locular, with axile placentation, indefinite ovules; stigma bilobed.

The Female Prothallus: The megaspore germinates *in situ* to give the female stage of the plant, as a wholly decadent individual, parasitic on the parental tissues (nucellus), and produced by 3 mitoses; represented when functional by 7 nuclei only, with definite relations, as a minimum organization, enough to do the work and no more.

The original nucleus of the megaspore (embryo-sac) divides, and the daughter-nuclei pass to the micropylar and chalazal ends respectively, there to divide again to 2 and 4, giving 8 nuclei in all. One nucleus of each group migrates towards the centre of the plasma, and the two fuse, or become closely approximated, as a *Central Fusion-nucleus*. The three left at the micropylar end differentiate as 2 *Synergidae* (sterile), and the functional female gamete or *Oosphere*. These surround with a denser film of cytoplasm, but are so far naked cells, with no walls. The synergidae are commonly a little in advance of the oosphere, underneath the micropylar canal, and the nucellus at this point is normally reduced to one cell-layer only. The three nuclei at the chalazal-end invest with cytoplasm and thin cellulose walls, as definitely osmotic, vacuolated, and absorptive units, nutritive in function, the *Antipodals*.

The Male Prothallus: Follows similarly from the germination of the pollen-grain (microspore) on the stigma; though the first stage may begin before it leaves the pollen-sac; pollen-tubes pushed out from the grain follow the stylar-canal, absorbing food-supplies from the stylar tissues, these being often specialized for the purpose. The growth of the tube is controlled by a *tube-nucleus*, produced at the first mitosis, and the other '*generative*' nucleus also passes along the tube: the distance travelled in some cases may be considerable, e.g. 10 in., and an inch a day is a fair rate for the growth of the tube. The latter follows style-canal and placental surfaces, reaching the micropyle of an ovule, and passing along it to the nucellus, apparently under chemical stimulus (chemotropic); the last directive stimulus possibly being due to the '*synergidae*'. Penetration between the cells of the nucellus is effected mechanically, and the end of the tube is brought into contact with the oosphere. The tube-wall is soft and gelatinous, and the contents of the pollen-tube, including 2 nuclei produced by division of the generative nucleus, are passed into the cytoplasm of the embryo-sac. These two nuclei represent the *male gametes*; and both are functional. The male prothallus is thus a still further decadent, coenocytic, and parasitic individual, represented by 3 nuclei, as the result of 2 mitoses.

Fertilization: One male nucleus attaches to the oosphere, and nuclear fusion (syngamy) takes place; the other passes on and fuses similarly with the central fusion-nucleus to give a *Triple Fusion-nucleus*.

Note. The first fusion is the sexual process, as a union of two specially isolated sexual units: the second fusion is only a vegetative approximation, since the central fusion-nucleus was not a gamete.

In the fusion of fertilization, the chromosome number is doubled, and the result may be termed a *Diploid Zygote*; the latter being capable of growth as a new individual.

The Zygote (oospore) immediately commences metabolism, the first effect being traced in the secretion of a cellulose wall, and vacuolation of the plasma: it thus becomes an osmotic cell, and begins to grow and divide.

There is no large *ovum* or motile spermatozoid in such a Higher Plant (although these are typical in many lower forms); fertilization-processes have been greatly simplified, the mechanism being termed *siphonogamic*.

Formation of Endosperm: the fusion of the second male nucleus with the central fusion-nucleus, though in no sense sexual, has a remarkable stimulating effect, and the Triple Fusion-nucleus initiates a series of rapid mitoses, giving a large number of nuclei scattering in the cytoplasm of the embryo-sac, and spacing out over the outer wall, as a parietal layer. Cell-walls appear delimiting cell-areas; and in this way, very quickly, a uniform layer of absorbing units is produced, taking food-supplies from the nucellus. Synergidae and antipodals are normally soon lost to sight among the new cell-formations, and the embryo-sac rapidly enlarges, as does also the whole ovule. From the primary system more tissue is produced by rapid cell-divisions proceeding inwards, as a thicker and thicker layer; in the general case filling the entire enlarged cavity of the embryo-sac with a mass of feeding-tissue, termed *endosperm*, as a special tract of new tissue parasitically absorptive from the nucellus.

Growth of the Embryo: The first division of the Zygote-nucleus (*oospore*) determines the orientation and polarity of the new individual; and of the two cells thus produced, the inner may be termed the *embryo head-cell*, the other is utilized as *suspensor*. Division of the latter gives a short filamentous series of a few units, with the effect of pushing the head-cell down into the cavity of the embryo-sac, where it can absorb food-material from the developing endosperm. The head-cell gives the bulk of the new plant, dividing symmetrically to 2-4-8 (*octant*-stage), and then becoming 2- and 3-layered by the addition of periclinal walls.

Differentiation of regions in the embryo 'head'-portion follows; 2 lateral lobes grow out (cotyledons), the apex of the stem is localized between them; while the apex of the primary root is marked out at the opposite pole, at the junction with the suspensor; the last cell of the suspensor being required to fill in the curve-pattern. Further elaboration of these growing-points follows the plan of the same regions in the adult. The primary root (Radicl) is thus orientated pointing to the micropyle.

Differentiation of Testa: The ovules with included endosperm and embryo grow to the full seed-size; the ovule with its contents constituting the seed-stage. An embryo being formed and differentiated, all subsequent modifications have reference to the manner in which it can be (1) nourished, (2) protected from desiccation, (3) ultimately separated from the parent plant, with (4) chances of being dispersed.

- (1) Increase of volume in the ovule may be considerable; ovules are commonly 1 mm., often less, and seldom over 5 mm.; seeds, as in Coco-nut, may be 6 in. long, with the same general proportions and parts. Nutrition is effected by increased formation of V.B. in the outer nucellus-layers.
- (2) The outer layers of the nucellus, as also integument, commonly add the effect of sclerosed cell-units, in utmost variety, as protective *testa*; the differentiation being continued over the entire surface of the ovule, without regard to special regions. The chalaza remains the base of food-supply.
- (3) With a view to separation from the parent plant, the chalazal region is normally sealed across by a special chalazal-plug, more or less similarly sclerosed, and an abscission-layer is prepared at the *hilum*, cutting across the funicle or base of attachment.
- (4) The ovule with its testa-layers, remains of nucellus, endosperm, and embryo, at whatever stage of growth it may have attained, is cut away as the *Seed*.

CAPSELLA (Shepherd's Purse), a small Crucifer weed, affords a convenient example of early embryology; the growth of the embryo being followed without section-cutting. The ovary is syncarpous, of 2 carpels; the 2 loculi containing 10-12 ovules each: on picking out these ovules from a green fruit, in a drop of water on a slide, and adding a drop of KOH and a coverslip, a gentle pressure will cause the embryos to 'jump out' of the turgid embryo-sac, and lie free in the liquid. A series of stages may be made out, beginning with the oldest and most easily obtained:—

- X. From full-grown fruits with seeds nearly ripe, a large embryo is obtained with well-differentiated radicle, and two green cotyledons bent sharply on the radicle (1 mm.) in the campylotropous ovule.
- IX. From younger fruits, 5 mm., a straight embryo, with two cotyledonary lobes, and radicle-apex with relic of suspensor, 360 μ over all, cots. half the length.
- VIII. Smaller fruits show embryos much smaller, with triangular or bilobed head as the first indication of cotyledons, suspensor-filament of 8 cells with enlarged bladder-like basal unit (150 μ).
- VII. Embryo with globular multicellular head (50 μ diam.) on a similar suspensor-filament: earlier stages require to be neutralized with H₂A to bring out cell-walls.
- VI. Head-region 40 μ diam., differentiated in 3 layers suggestive of embryonic meristems.
- V. Head-region 30 μ , 2-layered by first periclinal walls, and a few anticlinals.
- IV. Globular octant-stage, 20-30 μ diam., head-region marked with conspicuous cross: suspensor-filament of 5 cells, 18 μ diam., and basal bladder-cell 100 μ .
- III. Stage of quadrant-division (4 nuclei only), and first longitudinal wall (2-celled).
- II. Head unicellular (20 μ diam.), suspensor of 3-4 cells, lowest enlarged.
- I. Left for earlier stages not obtainable by this method.

Note: each stage adds a new construction-factor to the organism. Development is largely on mechanical lines until the outgrowth of the 2 cotyledons.

The Seed, as the essential factor in the life-history of the dominant Land-plant (Phanerogam), represents an ingenious solution of the problem of starting a new individual of the same class of organism as the parent plant rooted in the soil, so that the sexual stages as inherited from an older aquatic phase of existence are never exposed to the atmosphere, but remain completely enclosed in the plant-tissues, and protected within successive investments : i.e. :—(1) The ovary, as the latest departure of Angiosperms, encloses the ovules (megasporeangia) ; (2) the latter retain their sole residual megaspore ('embryo-sac') ; (3) the embryo-sac encloses the female prothallus in its vestigial construction : (4) of which one nucleus represents the female gamete. In the oldest environment of the sea the oosphere was freely discharged in the medium, to be fertilized by a flagellated spermatozoid, as are the ova of fishes to the present day.

To secure dispersal in the absence of any mechanism for the discharge of the embryo, the latter, enclosed in vestigia of embryo-sac, and ovular structures, is abstricted at the hilum, as the general case : provided with protective investment (testa) during its perennating condition, and supplied with food-material for use on germination, until it establishes a full autotrophic mechanism of leaves and root.

Storage of Food Reserves : Food-supply, once set going by the V.B. of the ovule, may be in excess of the amount required for immediate growth of the embryo, and hence accumulates to be utilized at a later date. The manner of deposition largely depends on the relative rates of digestion in endosperm drawing on nucellus, and embryo drawing on endosperm. If the endosperm is more active, it may fill up with supplies, and the embryo remains small (case of the endospermic or 'albuminous' seed). If the embryo digests supplies actively the endosperm may be poorly developed, all used up, or ultimately completely wanting in the seed-stage (case of 'exalbuminous' or non-endospermic seed). All grades occur : a state in which the endosperm is reduced to 1-2 layers only, and hence inconspicuous except in section, is very general. Endosperm is wholly wanting in seeds of most Leguminosae, and in Compositae. As general cases storage may be conspicuous :—

- (1) In Endosperm ; Grasses, Coco-nut, *Ricinus* (the oldest condition).
- (2) In Embryo, more particularly in massive cotyledons (Bean, Sunflower).
- (3) In parenchyma of the nucellus, as 'Perisperm', cf. Water Lily, Centrosperms.

Nature of Reserves : Mainly excess carbohydrate material, with smaller amount of proteid (nitrogenous reserves). Soluble materials are excluded (hence no nitrates, no potassium compounds, and no sugars) : general cases include :—

- (1) Carbohydrates as starch (Bean, Wheat, and Cereals) ; Cellulose, as almost solid wall (Date) ; Reserve-celluloses of many kinds (*Aucuba*, *Phytolaphas*).
- (2) Hydrocarbon fats, as compounds of fatty acids and glycerine : cf. Sunflower, Poppy, Rapeseed, Castor Oil, Palm Oil : the commonest case.
- (3) Proteid, localized in general cytoplasm of the storage cells, or in special granules (*Aleurone grains*) ; these may be differentiated in the dry seed, with crystalloid of globulin in ground substance (*Ricinus*, Brazil-nut).
- (4) Mineral Matter may be associated with such aleurone grains in special form of sphaerocrystals, as the 'globoid' of CaMg Phosphate.

Perennation of the Seed : The embryo passes into a resting stage ; food-supplies are checked, the V.B. is plugged off at the chalaza, and the scar of the hilum is protected in continuity with the testa-layers. The seed loses water, and dries off, often shrinking to half its volume : successful perennation is usually associated with extreme conditions in this respect. Great range of variation obtains : cf. minute seeds of Willow, and massive seeds of Horse-chestnut, with little vitality if dried. The general mechanism may be masked by new departures ; cf. fleshy fruits as Apple, cut off with seeds enclosed to rot on damp ground ; Fig, whole inflorescence cut away, edible, rotting, or animal-dispersed. The abstriction of an air-dry, wind-borne seed is the primary condition for Land Flora.

Life of the Seed : Metabolism is reduced to a minimum, but some sort of katabolism must continue : little evolution of CO₂ can be checked in air-dry seeds, or absorption of oxygen, katabolism is intramolecular ; i.e. changes are too small to give an appreciable gaseous exchange, and life may be prolonged a considerable time at expense of stored material. No seed has been known to live 150 years (few 100-50).

Vitality may be shown by curve for germination-capacity for a few years only; most seeds die within a year or two if kept dry. Seeds buried in damp soil without oxygen probably deteriorate more rapidly: a dead seed does not germinate, and conversely.

(1) **Phaseolus** (Kidney Bean): Smooth coloured testa with conspicuous lateral hilum; soaked seeds increase to twice their volume dry, showing micropyle at one end of hilar scar (7 mm.), and chalazal knob at the other. No trace of endosperm; leathery testa enclosing embryo with 2 massive cotyledons, small radicle, 4 mm., pointing to micropyle, and plumule (5 mm.) with young leaves folded, between cots. Section of cots. shows uniform parenchyma (100–150 μ diam.), with rather thick walls (6 μ), and abundant starch-content; grains oval, 30–50 μ , with central hilum; also granular proteid. Testa non-lignified, with conspicuous prismatic layer on surface; cells much thickened, small basal lumen (70 μ by 10).

Vicia Faba (Broad Bean) essentially similar, with black hilum, flatter cotyledons, radicle conspicuously outlined.

(2) **Helianthus** (Sunflower): *Fruits* sold for 'seed'-purposes are dry achenes, indehiscent, enclosing one seed:—crack off fruit-wall from soaked 'seeds' to see membranous testa, relic only, no endosperm, straight embryo, with adpressed cotyledons (9 mm.), straight radicle (9 mm.), and minute pointed plumule. Section of cots. shows no starch, but abundant fat (running to oil-drops on adding KOH) in thin-walled cells (40 μ or so) grading to 3-ranked palisade on upper surface (100 μ deep).

(3) **Aucuba**: Scarlet berries particularly good in spring months; each containing one large seed, not dried off: testa thin and undifferentiated; endosperm an ovoid mass of thick-walled pitted cells, with aqueous contents and little fat. Embryo small, but accurately centred at apex below stigma of fruit, and cut in median plane: rounded radicle, and plumule, with good apical differentiation, as cleared in KOH. Adapted for germination at the forest-base.

(4) **Ricinus** (Castor-Oil Plant): Dry seeds with glossy marbled coat, with 'caruncle' growth over micropyle. In soaked seeds note testa of 1 densely sclerosed prismatic layer (peripheral layers dried off), only cut in developmental stages of green fruit, and residual inner parenchyma as white skin, enclosing cake-like mass of endosperm of thin-walled parenchyma (about 50 μ) storing fat and aleurone grains. Embryo with two thin, veined, cots. laid out in median plane, following shape of endosperm; small radicle and plumule. Sections of endosperm, cleared in ether, mounted in water, show aleurone grains (10–12 μ), many in each cell, differentiated into crystalloid of globulin, and a globoid (3 μ). Salt-solution on spirit-material dissolves the crystalloid; the rest of the grains cleared in KOH, and the globoid of CaMg Phosphate in acetic acid. A xerophytic tropical seed.

(5) **Aesculus** (Horse-chestnut): largest available tree-seed in autumn; 1½ in. diam., testa thick (1½ mm.), no endosperm, embryo massive. Broad hilum (20 mm.) with pattern of radicle at one side gives orientation for cutting in median plane: note radicle in pointed pocket-like end of curved ovule, plumule, and cotyledons, often with central space imperfectly filled; cots. store starch as oval grains (15 μ) in 80 μ parenchyma. Testa non-lignified, stained with tannin, of small units, little differentiated. Seed not dried off.

(6) **Juglans** (Walnut): Most elaborate seed of available tree-types (autumn). In soaked 'seeds', note 'shell' = sclerocarp of a Drupe-fruit, cracking in 2 valves (not carpellary portions). Seed, removed from 4 pocket-chambers of fruit, separated by cartilage-partitions, shows 4 main lobes; each cot. bilobed, and lobes crumpled or convoluted irregularly. Cotyledons orientated in same sense as the shell-valves: to see both, and plumule, cut across in plane at right angles to dehiscence-line. Main root-apex at pointed end; plumule with leaf-rudiments. Section of cot. lobes shows food stored as fat in thin-walled parenchyma; testa of vestigial layers, V.B., and aqueous epidermis (60 μ); endosperm relic, of 1–2 outer layers, storing fat, following the testa and peeling off with it; seed not dried off. In development the endosperm is formed as a scanty lining, and the cavity of the seed is filled with fluid (July). The gelatinous endosperm is replaced by embryo (August), and the cot. lobes extend to fill the pocket-cavities modelled in the massive ovary-wall.

(7) **Hedera** (Ivy): seeds small, 3–5 in 'berry'-like fruit, each covered by parchment-like sclerosed sclerocarp. Testa thin and membranous; embryo small; endosperm stores fat, and is *ruminated*; rain-washed pyrenae suggest grains of corn.

I. In response to stimulation by fertilization (often by pollination only), **Growth-phenomena** may obtain, associated with conduction of food-material towards various parts of the floral axis, starting from the ovules and ovary-chamber; the latter enlarges in order to contain the developing seeds, and is more or less specialized in connection with the necessity of protecting these from desiccation. The general methods are:—(1) increase in volume and mass of tissues; (2) aqueous tissue storing water in virtue of osmotic cell-contents; (3) sclerosis of protective lignified regions; (4) associated with general storage of food in living cells as they cease growth.

II. **General Theory of the Carpel**: The carpel regarded as a leaf folded on its upper surface to form the ovary-chamber, for protection of ovules to seed-stage, opens out at their maturation, in order to discharge the latter: (1) by an active growth-movement; (2) by the physical tensions of dead tissues.

III. The simplest fruit is thus that of the many-ovuled apocarpous carpel (= **Polliole**), e.g. Columbine, Monkshood, *Helleborus*, etc.; the suture is opened up as the wall dries, and seeds are passively shed from apical aperture downwards.

A more special case is the **Pod** (or legume) characteristic of the family Leguminosae; the single flattened carpel opens by the suture, but also splits along the opposite edge (midrib-line) giving 2 'valves'; these contract symmetrically, in spiral curves, and the seeds are set free by 'torsion'-effect, thrown some distance (10–12 ft.): cf. Pea, Bean, Furze, Broom, *Laburnum*, *Robinia*.

IV. **Syncarpous Ovaries**, retaining indications of vestigial carpels, may open more or less in terms of the original units, giving *valves* of the same number as the carpels, or twice as many (cf. pod); or the apertures reduce to *pores*: constituting a vast variety of **Capsules**. In such note:—number of carpels indicated; placentation; number of seeds; mode of dehiscence, (a) along old lines; (β) along new lines, the simplest case (*loculicidal*) opens up the cavities directly (Lily).

In the case of 'inferior-ovaries' the lines are necessarily quite new (Iris): in the case of Crucifers, 'valves' are cut out of a framework. Many other elaborate constructions of the same kind (cf. Mahogany). Syncarpous ovaries in the limit may open along lines which ignore the old construction altogether; cf. 'Pyxidium', by a transverse lid; the case of portions of the ovary split off (Schizocarps), and the individual portions containing 1 or more seeds (Mericarps, and 'Cocci').

V. More specialized in another direction are those which no longer dehisce at all (Indehiscent); saving the trouble, especially when containing only 1 seed, and striking out new lines: Special cases:—

(a) the entire wall is sclerosed more or less, and incapable of opening; if small and feeble, the case of the **Achene**, including small and deteriorated cases (*Helianthus*, Rose, Buttercup).

(β) if large and woody (to be 'cracked') the case of the '**Nut**' (Hazel). Points to note are again, the number of carpels, mode of placentation, superior or inferior ovary, number of seeds, typically reduced to 1; the method readily following reduction of ovary-contents (Acorn).

Note every indehiscent ovary was once dehiscent, as every syncarpous ovary was once apocarpous.

VI. More elaborate methods, involving succulence and water-storage (by osmotic acids) in parenchyma of the ovary-wall, give the case of the **Berry**; in which, before death of the tissues, acids may diminish, starch turn to sugars; striking pigments may appear (anthocyan, carotin); the fruit becomes conspicuous and attractive to animals as food. The Berry in various forms; typically in the Grape (sup: 2), Currant (inf: 2); *Note* the number of carpels, and whether superior or inferior. Special cases as the Orange (sup: 9–11), Banana (inf: 3), Melon (inf: 3).

VII. More specialized still, as combining the two last methods, with succulent external region (Sarcocarp), and sclerosed internal zone (Sclerocarp), often marked off by median V.B. system. In such case the sarcocarp is attractive and conspicuous (edible), the sclerocarp becomes more useful as protection against damage to enclosed seed (usually 1 only). The case of the **Drupe**, typically seen in Plum (sup: 1) and Cherry, Peach; less marked in Almond (non-edible and still dehiscent); as also in Walnut (inf: 2), and Coco-nut (sup: 3) with fibrous husk.

The special case of several loculi, each protected by sclerocarp separately, gives a Drupe with several 'stones' (= Pyrenae, e. g. Holly (sup: 4), Ivy (inf: 3-5).

Note. Secondary biological adaptations utilize old structural factors regardless of their original significance. Above simple generalizations are based on familiar types of N. Temp. zone, and have little bearing on the immense variety of the Tropics.

VIII. So far included types of simple ovary-construction (= Pericarp): Similar growth-effects passing on to other floral-regions (e. g. receptacle) give varied types of **Receptacular Fruits**; especially noted if these also become edible: cf. Strawberry with achenes; Apple, Hawthorn.

IX. The idea may be extended further to the case of **Pseudocarps**, in which the growth again becomes edible, and involves the entire inflorescence-region (Pineapple, Fig, Bread-fruit); if not edible the effect is rarely noticed (cf. great head of Sunflower in fruiting condition).

Note. Facts are more important than names; details of special cases are infinite, and above generalizations are quite elementary.

Beyond protective adaptation (essentially xerophytic), the evolution of the fruit-mechanism depends on the necessity for the abscission and discharge of seed, fruit, or associated structures, with provision for **Dispersal**, away from the vicinity of the parent plant (in the normal case perennial). Mechanism of Translocation, (1) provided by plant itself, (2) physical movements of wind and water, (3) locomotor agency of animal life (clearly the most special case).

Note. Preceding mechanism may be (1) utilized, (2) intensified, as the adaptation of something previously existing. Vestigial structures take on a new lease of existence. Present adaptations may be so perfect that they are initiated at an early date, and so appear 'prophetic', with no preceding significance. Perfect mechanism, isolated by competition, may leave no trace of intermediate stages.

I. Examples of auto-discharge:—

(a) Bymechnism of Turgidity: *Impatiens*, *Ecballium*: including contact-stimulus.

(β) Tensions of lignified tissue: *Viola*, Pea-Pod, *Geranium*, Spurges, *Buxus*.

II. **Neglect** of special precautions (general in indehiscent fruits), achene, nuts, etc., left to physical chances: e. g. wind drifts sand and stones, according to velocity; any seed may be so shifted: flotation on water; many float more or less till soaked without special modification; just as others may be carried in earth attached to living organism. Interest centres in special adaptations: the greater as the more complex in co-ordination of morphological, anatomical, or biological details.

III. **Wind**: utilization of rounded form for rolling; flat forms as 'planes'; idea emphasized in 'wing' extensions of seed (α), of fruit (β), of accessory structures (γ): cf. *Pinus*, *Oroxylum* (α); Ash, Sycamore, Elm (β); *Tilia*, *Carpinus*, Dipterocarp (γ): Utilization of Hairs; tufts, plumes, parachutes, on seeds, fruits, or accessory structures; cf. pappus of Thistle: cases innumerable, each to be investigated independently for (1) nature of structure; (2) origin of mechanism; (3) efficiency. Cf. *Salix*, *Populus*, *Platanus*, Cotton. Also combined with small seeds, hairs, or wings.

IV. **Water-flotation**: seeds or fruits with impermeable cuticle, cork-floats, air-lacunae (*Alnus*, *Iris*): Special cases; gas-evolution (*Nymphaea*); air-chamber (Coco-nut): Note time of floating; chances of germination.

V. **Special utilization of Animal locomotion**: Burr-fruits; spinous fruits, recurved hooks, thorns of xerophytic types. Hooks from styles, emergences on ovary-wall; accessory emergences on calyx, bracts, etc. (Burdock, *Galium*).

VI. More significant, **Internal Dispersal of seeds of 'Edible' fruits** by birds, bats, monkeys, man. Highest animals and highest plant-types co-ordinated Correlated adaptation (1) in fruit, as colour, scent, taste, food-value, sugar, oil; 'ripening' as incipient decay: (2) in seed, to resist trituration of bird, or digestive enzymes of animal; cellulose endosperm, protective testa, sclerocarp, etc.; (3) adaptation in animal; dentition, size of bird and size of berry; 10 mm. diam. for British birds. Dispersal with a margin of loss, as by squirrels, rats, ants.

Note, dry dehiscent fruits begin to appear as archaic relics.

Effect on vegetation of the human race, still essentially fruit-eating, in terms of dry fruits of cereals, beans, etc.; cultivation of a few races, others regarded as 'weeds'; tendency to eliminate indigenous flora.

GERMINATION: The renewal of normal active metabolism on the part of the resting embryo ('*germ*' of older writers); hence also applied to the active growth from a spore, and even from a perennating structure, as secondary application.

Dependent on physical environment, in terms of temperature, oxygen-supply, and water-supply; three essentials all requisite, implying normally well-aerated, damp and warm soil, as characteristic habitat of a land-plant; in case of very hard seeds also dependent on the permeability of the testa-layers.

Water taken up by imbibition of colloidal cell-membranes, leads to imbibition by colloidal plasma, and osmotic activity soon implies turgidity of all living units. Food-supplies for katabolism and growth are requisite before the photosynthetic mechanism can get to work; hence the more food on hand the better; all insoluble reserves require to be made soluble before they can be conducted. This is effected by the action of enzymes also liberated by addition of water to the plasma.

Enzymes are proteids with catalytic activities, hydrolyzing or oxidative, hastening chemical change: living plasma is its own catalyst, but enzymes secreted by plasma may be active outside the cell producing them, and may be brought to bear on material (as a massive starch-grain) not in immediate contact with living plasma. Different classes distinguished according to material acted on, as (1) *Diatase*, hydrolyzing starch to sugars (including invertase); (2) *Cytase*, hydrolyzing reserve-celluloses to sugars; (3) *Lipase*, hydrolyzing and oxidizing fats, to sugars in part; (4) *Protease* breaking down proteids to amino-acids, etc. Different enzymes in different seeds according to reserves, and often produced in special cells; e.g. enzymes of embryo may be secreted into endosperm-tissue (largely inactive), rendering its reserves rapidly soluble.

Fatty Reserves: the general case, stored in embryo or endosperm; fat rapidly disappears, much free oxygen being used up in the process: cf. palm-oil of *Elaeis* kernels, used for margarine: glyceride of palmitic acid, originally of glycerine and 3 chains of palmitic acid, each 16 C atoms, with separation of $3\text{H}_2\text{O}$: first hydrolyzed back to glycerine and the free acid; the latter oxidized in part, and broken up to sugar groups, etc., cf. full structural formula.

Starch Reserves: good example in the malting of barley, for maltose (malt-sugar, disaccharide): cf. *Zea Mais*. Main mass of endosperm packed solid with starch; embryo at basal end, with radicle in sheath (coleorhiza), plumule with first sheath-leaf (coleoptile), cotyledon, one only as *scutellum*, an absorbing organ with V.B., lying in contact with the endosperm as a broad shield-like tract of parenchyma, with superficial layer of columnar cells ('palisade'): the latter secrete an active diastase into the floury endosperm; the polygonal starch-grains, on testing with iodine, show corroded spots and lines (white on the blue grain), and the grains break to fragments and dissolve, giving soluble dextrins (polysaccharide), maltose (disaccharide), and ultimately by maltase to dextrose (monosaccharide). The soluble materials are absorbed by the scutellum cells, and passed on to the V.B.: when conduction cannot cope with the supply, transitory starch-grains are seen in scutellum-parenchyma, but not in the palisade-cells. *Note* that the peripheral layer of the endosperm, digestive in the growing seed, stores no starch but aleurone-grains with globoids of phosphate.

Emergence of the Embryo: The radicle, as important for continued auto-absorption of fluid, emerges first; the tip is normally pushed out at the micropyle by elongation of zone ii, and if incorrectly orientated the latter adds a geotropic curvature (positive). Further elongation of the *hypocotyl*-region normally draws out the cotyledons, and this region puts in a geotropic curvature (negative), if not previously erected, pushing the cots. above the soil. The latter diverge (normally 2 in Dicot. type), and the plumule continues the further development of the shoot-system.

Note, for penetration of soil by root-apex some resistance is requisite, hence necessity of the weight of a certain amount of soil; if insufficient the seed may be lifted above ground; well-developed cotyledons commonly carry up the old seed-coats. The hypocotyl is neither stem nor root; its vascular system links up the stelar organization derived from two opposite growing-points. Intercalary extension of this hypocotyledonary axis is utilized in normal *epigeal* germination with photosynthetic cotyledons.

In large seeds with massive reserve-storing cots., as the most advanced seed-stage, as also in many special types, the cotyledons are not so extracted, but remain permanently under ground within the testa. In such case germination is *hypogeal*; the hypocotyl remains short, and the plumule erects directly; cf. Oak, Chestnut, Horse-chestnut, Broad Bean; also in Monocots. with massive endosperm (Date, Coconut, Grass-type), the single cotyledon acting as haustorium.

Cotyledons and Juvenile-leaves: Two symmetrically-paired cots. are normal for Dicots., as great majority of Angiosperms: a single terminal cot. in most Monocots. The shape of the cot. is determined largely by space-factors, foldings, etc., in the seed-cavity, and is often markedly different from the later-formed leaves (Beech, Sycamore). The first leaves of the seedling may be also different from later formations, usually presenting a simpler type of organization; i.e. entire instead of lobed or compound; hence termed 'Juvenile-leaves'; but in specialized forms recapitulatory stages of more elaborate leaves may occur; cf. trifoliate seedling leaves of *Ulex*, more marked in the fully pinnate seedling leaves of phyllodinous Acacias.

LIFE-CYCLE. With the growth of the Seedling a new individual is established, absorptive and photosynthetic like the parent-form of soil-plant. The sequence of reproductive stages may be tabulated in such a scheme as:—

I. The conspicuous land-plant to which the name is given bears reproductive shoots as:— **Flowers;**
 With reproductive leaves, or
sporophylls of two kinds, as:— . **Stamens (micro)** . . . **Carpels (mega);**
 these produce
sporangia of two kinds, as:— . **Pollen-Sacs (4, micro)** . . . **Ovules (1 or many, mega);**
 and these in turn
spores of two kinds, as:— . . **Pollen-grains (micro)** . . . **Embryo-sac (1, mega)**
 The spores as uninucleate cells close this stage, and they are so far *asexual*, since there is no fusion; the plant bearing them is *asexual*, as a spore-producing *sporophyte*-generation.

II. The spores germinate to prothallial stages, as decadent, coenocytic, somatic organizations, as:— **Male Prothallus** . . . **Female Prothallus**
 (of 3 nuclei) (of 7 (8) nuclei)

Certain nuclei are set apart as sexual units (*gametes*):— **Male nuclei** . . . **Oosphere.**
 These unite by an act of fertilization (*syngamy*) to:— **Oospore (Zygote)**

The oospore is a uninucleate spore closing this sexual stage, and it germinates directly to give the **Embryo.**

The plants producing the sexual cells are so far sexual, and may be termed *gametophyte*-generation. The fact that the embryo is closed down to a dormant stage in the seed, does not affect its nature as the new young plant, aroused in germination to get a hold on the soil. The seed-stage is a biological addition of little significance in the life-cycle of reproductive phases.

The life-cycle thus presents the alternation of a sporophyte stage with a gametophyte stage, though the latter is very decadent, and so vestigial that it is hard to follow. The sporophyte generation has diploid nuclei, up to the mother-cells of the tetrads; the gametophyte has haploid nuclei. Fertilization doubles the chromosome number; meiotic reduction occurs in the elaboration of asexual spores.

Phaseolus, seedling 2-3 weeks old; note strong erected shoot-axis with rapidly elongating first internode; juvenile foliage-leaves with stipules; main tap-root with laterals; testa ruptured, cotyledons hypogeal at first, coming above ground in later stages and developing chlorophyll; practically no depletion of starch reserves at this stage. Short hypocotyl; buds in axils of cotyledons, growing if first leader is damaged. Section of primary root and epicotyl gives primary arrangement of tissues.

Helianthus: 2 green oval cotyledons, divergent and photosynthetic, carried up by intercalary extension of hypocotyl, 3-4 in.; root-system feeble, 'fibrous': transv. sect. of cotyledon shows green lamina with palisade, and practically no fat left: reserves rapidly metabolized.

VEGETATIVE MULTIPLICATION, as natural propagation in terms of increase in the number of individuals, may occur in cases of special adaptation, to secure dispersal of more or less readily detachable portions of the organism; the latter regenerating the missing parts, and establishing new individuals.

(1) Buds detached as gemmae, **Bulbils**, small or even large stem-tubers, borne on overground shoots: cf. bulbils in leaf-axils of *Lilium tigrinum*; leafy buds or young plant-shoots borne on foliage-leaves, *Nymphaea*, var.; many ferns as *Asplenium bulbiferum*; *Bryophyllum*; small axillary tubers of *Picaria*, larger tubers of *Vitis pterophora*, 6 in.

(2) **Vivipary**: often applied to the case of similar buds, found growing out in green leaves, produced in the inflorescence-system, and replacing flower-buds; cf. *Allium* sp.; 'viviparous' varieties of grasses, more particularly in alpine conditions.

(3) Tips of decumbent branches, rooting on contact with soil; general in Brambles, with abundant adventitious root-system, and death of intermediate portion: occasional in trees, as Spruce, *Castanea*.

(4) More general case of **Stolons** and 'Runners', giving radiating systems, the laterals rooting and separated by decay of intervening portions, as a method of seeking new ground close at hand; specialization of 'runners' implies great internodal extension, cf. Strawberry. Laterals readily detached, *Sempervivum* and many Cacti (*Mamillaria*, *Echinocactus*-types, rolled by wind, or attached by hooks to animals).

(5) Similar extensions as adventitious buds from surface-roots, the case of 'Suckers', often at great distance; for herbaceous plants giving clustered habit (Nettles, Raspberry, Roses), small trees as Hazel, Plum; or forest-trees as Elm, Poplar, giving natural regeneration.

(6) More effective dispersal of perennating subterranean portions, as readily detached laterals of bulbs, corms, tubers, in sandy soil, with special adaptation for wind-rolling.

Cultural Propagation gives more remarkable effects, as in:—

(1) Division of the root-stock (rhizome-system) of herbaceous perennials presents no special feature, all parts being present.

(2) 'Sets' and 'Cuttings' include the case of stem-portions only being taken, as stakes of woody plants, sets, or shoots of more herbaceous parts as cuttings: simple experimental origin, more effective in warm climate, poles and stakes of green wood send out adventitious roots (Willow, Tamarisk) and regenerate a root-system, given food-storage in main axis.

(3) Herbaceous cuttings, as general case, more elaborate; the wound is healed by a phellogen giving 'wound-cork', and relieved from the tension of the outer tissues, in good supply of free oxygen, active growth of parenchyma produces a cushion-mass of tissue ('callus'). From such active tissue, given food-supply of storage or photosynthesis, adventitious roots arise endogenously, and regenerate the root-system; cf. Geranium cuttings; Essential factors, exposure to air for healing of the wound, food-storage in parenchyma ('ripened' shoots), damp air to restrict loss of water till new roots are established, optimum temperature to shorten the period of regeneration.

(4) More marked cases of 'Regeneration', as root-cuttings which reproduce new shoot-systems from endogenous apices (*Dandelion*, *Calystegia*); and even leaf-cuttings (*Begonia* sp.) regenerating both new stem-apices and roots from undifferentiated callus-parenchyma.

(5) **Grafting**, a more complex case, suggested anthropologically by striking a cutting in another plant instead of in soil; more effective in favourable climatic regions, and the general method of plant-improvement among the Chinese and Romans (*Columella*): cf. 'Plug-grafting', still in use in the case of the Olive of S. Europe: 'Inarching', observed in nature for branches of same tree, or adjacent one, pressed together by weight; imitated by tying stems together until united at cambiums; can be done when the leaves are on (Vine), 'graft by approach'.

cf. Parasitism of *Viscum* (Mistletoe) and other *Loranthaceae*, as 'natural grafts'; the parasite making haustorial connexion with the xylem and water-supply of the host; i. e. taking only transpiration-current and non-colloidal diffusible material (not proteid)

'**Budding**,' as used for propagation of Roses: a young bud, with attached cambium-layer 'shield', slipped in T-opening of cortex of another stock: the cambiums unite and the wound heals leaving bud attached to stock.

Stem-grafting: a young shoot with buds (*scion*) cut to fit stock, in form giving broad range of cambial approximation (cleft-grafting, whip, and 'saddle'-grafting); the whole kept warm and damp to reduce transpiration, until the wound is healed (clay, wax, or earthing-up). Utilized for Fruit-trees, Conifers as *Araucaria*, *Cupressus*, and Forest trees. Plants are said to be 'worked' on the stock. Many vars. may be put on the same individual: cf. *Ornus* on Common Ash, *Mespilus* on Hawthorn, *Zelkova* on Elm, *Corylus Colurna* on Hazel.

Root-grafting, often more effective since the whole may be kept damp in well-aerated soil; cf. *Clematis* vars., *Paeonia*.

Herbaceous Grafting, more readily effected when the tissues are of undifferentiated parenchyma and cambium is active; cf. Tomato on Potato, Cucumber on Veg. Marrow; less useful owing to short life of host: more effective in case of many succulent Cacti.

Theory of Grafting: The cambiums and parenchymatous tissues of graft and stock unite in a common wound-callus; this may differentiate wound-tracheides putting the water-supply in continuity, but always making a more or less *bad join*; no primary connexion of vessels or sieve-tubes; only water and solutions pass to the scion, hence water-supply of latter is always pinched at the junction; tissue-union may be more complete later. Consequences follow: the water-supply of the scion is affected by that of the stock; e.g. a stock with vigorous root-system may give a scion of xeromorphic habit a better supply than it had before; the graft then grows vigorously ('enlarging'): more usually (commercially), on a stock with less root-activity, the scion is distinctly more xerophytic than before, and the balance of photosynthesis against proteid-synthesis is increased;—e.g. giving (1) reduced vegetative growth, (2) early flowering, precocity in fruiting, (3) abundant fruiting, (4) fruits larger, sweeter, and often more highly-coloured (anthocyan and carotin pigmentation), hence 'ennobled'; cf. Apples worked on a stock with fibrous roots, Pears on Quince.

Note: Similar periodicity is more essential than affinity (*Columella*), but in inferior climate the latter is the readiest way of getting the former. Merely grafting a shoot back on the same individual gives an improved effect; the result may be emphasized by 'double-grafting'. Similar 'ennobling' phenomena may be produced by ringing the tree, or constricting the cambium by tying a string round it.

Influence of the graft on the stock, and *vice versa*, is apparently confined to the translocation of readily diffusible substances; but interesting cases may be noted; cf. variegated Laburnums. Connexion is solely nutritive.

Plant Chimaeras: Of great interest as bearing on the question of the union of cells and plasma of scion and stock. Commonest case is that of *Cytisus Adami*: *C. purpureus* grafted on common Laburnum (1826) gave a shoot intermediate in all respects, in branches, leaves, flowers, and inflorescence-characters, so far unlike a hybrid. Also marked reversions to the two 'parents', so that 3 types of branch, leaf, and flower, in different colours, are produced on the same tree. Propagated still by grafting *C. Adami* on Laburnum.

Cf. also *Crataego-Mespilus* of Bronvaux (Metz), as Medlar on Hawthorn, with 5 types of flower, 2 components, and 3 intermediates.

Explained by 'Chimaeras' of *Solanum* on Tomato (Winkler, 1908); herbaceous grafts with free production of adventitious buds from stock when headed back. On cutting back a grafted specimen through the graft-junction, occasionally a bud starts on the line, with apex compounded of cells from either side; the resultant shoot may be a *Chimaera*, of one type down one side and the other type on the opposite side, even to demarcation along one leaf of the spiral phyllotaxis common to both. Others give more intimate fusions, cf. sectorial, periclinal, and blended Chimaeras: these also show phenomena of reversion, and *C. Adami* is regarded as a *periclinal chimaera*, with the Laburnum cortex and stele enclosed in *C. purpureus* dermatogen. *Note*, however, that reversion to the latter is still obscure, as also sectorial reversion (cases may vary in different apices). Protoplasmic continuity obtains between all the tissues; hence may illustrate vegetative union or *plasmogamy*, as opposed to *syngamy* of a true hybrid.

Analogy of Higher Animals: The historical line of approach : cell-units set apart for reproductive purposes in early ontogeny of animal, with special developmental history as 'gametes', differentiated in two forms ('sex'-distinction) as :—

- (1) A smaller (microgamete), $5\ \mu$ or so long, uninucleated, active, with long flagellum acting as a posterior propeller, spermatozoon, or *male* gamete produced in enormous numbers.
- (2) A larger (megagamete), as an immotile spherical cell, uninucleate, $200-300\ \mu$ or more diam. (or even 1 inch diam. in yolk of hen's egg, enormously distended with reserve food-storage as proteid and fat), the ovum, or *female* gamete ; produced in small numbers.

Note: 'Sex' terms, originally applied to the differentiation of the body of an animal producing the gametes, as 'male' and 'female', are transferred to the organs in which the latter are developed, and in more recent times to the gametes themselves, as a quite secondary application.

Fertilization, by fusion of two such gametes, extending to fusion of the nuclei (syngamy, nucleogamy), gives a Zygote, as a new cell-unit with single control. A rejuvenated cell is thus produced capable of initiating growth and metabolism as a new organism of the same general class.

Note: Gametes are cells set apart for this special function, and are non-metabolizing units, working in terms of stored food-material, if at all, hence short-lived, and normally soon dying if not used for fertilization. Exceptional cases, more frequent in lower organism, imperfectly delimited for the function, may continue metabolism, presenting phenomena of so-called 'parthenogenesis' or *apogamy* (cf. ovum of Frog, and oosphere of *Fucus*, apogamy may be induced artificially).

Meaning of Sexual Fertilization: Fusion of cell-units of different individuals dates to most remote phases of living organism (in the sea), few phyla being wholly without it (Bacteria): apparently advantageous from several distinct standpoints: (1) By blending the experiences of two lines of descent, it improves the outlook of the new *individual*; (2) affording a new stimulus to development; (3) repeated mingling tends to balance up the average of associated individuals, and so establish the *racial* standard; (4) it makes for variation owing to subsequent necessity for *meiosis*; (5) hence may be regarded as the initiator, hastener, and regulator of the '*race*'.

Sexual Reproduction in Plants: Higher plants follow a closely similar progression, but tend to become much more complex. The union of a flagellated male gamete (*antherosoid*) with a large immobile female gamete, held in spherical form by surface-tension (*oosphere*), as zoidogamic fertilization, occurs in Brown Seaweeds as in spawning fishes, in the sea; but is less obvious in higher Land-plants, being replaced first by Fertilization *in situ* (archegonium of Fern), then by loss of the flagellated mechanism, and fertilization by a tube (Siphonogamy) in Angiosperms. All the sexual processes are henceforward of microscopic dimensions, and are enclosed within the tissues of the plant, as a means of protection against desiccation on exposure to air. Other problems have to be taken into account.

Asexual Reproduction: Plants, as opposed to higher animals, being permanently fixed organism, the necessity for Dispersal at some stage introduces another factor; more particularly as the attainment of fertilization *in situ* eliminates any chance of dispersal on the part of the female gamete.

In Land-plants a stage of special unicellular units, set apart for this purpose as air-borne spores, replaces a preceding condition in the sea of water-borne spores, and still older flagellated zooids which do not fuse (apogamous); such spores being cells with a nucleus, borne in a special organ (sporangium), and liberated into the external medium by dehiscence of the sporangial wall.

Alternation of Generations: To cover all these functions in sequence, a state of alternation is set up, as one individual is set apart to produce the asexual spores (sporophyte generation); and the next one (the gametophyte generation) bears both male and female organs, or only one set (σ^7 or φ). A generation is defined as a phase beginning with a uninucleate cell (spore), and ending with the production of a similar state (sexually or asexually produced); and such a unit gives rise to the complementary phase.

The Life-Cycle includes the enumeration of the sequence of such phases; and this may become further complicated in Angiosperms by differentiation in the sporophyte generation of 'micro' and 'mega' states, much in the manner of sexual differentiation.

Note: The term *sexual* is often transferred from its original meaning of 'sex'-*distinction*, to the process of the nuclear fusion (syngamy).

Theory of Wastage: The Life-History of the Angiosperm represents the gradual perfecting of the mechanism of reproduction over a long sequence of environmental changes, in which all such processes involve an enormous loss to the organism as wastage. The diminution of such wastage is the criterion of higher organism; but as one method of wastage is corrected in advancing races, so a new one, probably still greater, may be introduced. Three main sources of wastage may be traced in Angiosperms.

I. Sexual Wastage: In the oldest phase of algal life in the sea, as organism of single cells, sexual fusions would involve a wastage of 50 per cent. of the individuals, even admitting the extremely vague chance of finding another gamete; while the chance of the zygote ever finding a suitable substratum may be practically nil.

- (a) Apogamy, or **Asexuality**, saves the wastage of the fusion-function, but is still open to that of dispersal.
- (b) **Fertilization in situ** saves the wastage of the female gametes with the food-supply of the zygote (all Land Flora, as Archegoniatae).
- (c) **Siphonogamy** saves the wastage of the male gametes (higher Gymnosperms, and absolute in Angiosperms).

The sexual process is ultimately freed from wastage, and this problem is solved.

II. Asexual Wastage: In Land-plants the asexual spore is subjected to a new form of wastage of air-borne spores, even worse than anything in the sea. The spores differentiate into smaller microspores, and larger megaspores as food-storing units. The latter are ultimately no longer shed, but are pollinated *in situ*, resulting in the seed-stage as a direct consequence, hence:—

- (a) The **Seed-habit** saves the wastage of the megaspores, but the microspores are still wasted owing to wind-pollination being vaguely efficient.
- (b) **Entomophily** solves the problem of the wastage of the microspore; the more as the pollen-grains are taken all together and placed exactly where wanted, none being lost in transit (cf. Pollinia of Orchids); but in no case as yet absolutely without some loss (as in non-visited flowers).

III. Embryo Wastage: Though the seed-habit saves the megaspore from being wasted on discharge, the embryo has still to be detached at a later date for dispersal purposes, and wastage falls all the more on this stage. Hence the greatest wastage of the Angiosperm is now expressed in terms of lost seeds (notwithstanding the solution of intervening problems), the original difficulty being shifted a step further on, and still unavoidable. Such wastage is expressed in:—

- (1) Failure to find unoccupied ground.
- (2) Chances of death by desiccation on the way.
- (3) Competition on germination with other types of organism.
- (4) Competition with organisms of the same class (i.e. species).

These conditions may be compensated by:—

- (1) **Effective dispersal mechanism**, and means of transportation; hence expressing the value of the smallest advantage in terms of wind or animal agency.
- (2) **Effective protective investments** of testa, fruit-walls (indehiscent fruits); sclerocarp of drupes; sclerosis of nuts, &c., as many of the most advanced types of **xeromorphic fruit-organization**.
- (3) **Storage of large quantities of food** for early stages of the seedling; rapid digestion of reserves, exalbuminous seeds, hypogeal seeds; including the more specialized, higher, types of **seed-organization**.
- (4) The most difficult problem, supposing organisms of one race or line of descent are identical; but the individuals produced by sexual reproduction are not exactly alike one another, or the parents, and do not start on equal terms. Hence the value of even the smallest **variations**, the latter being apparently introduced in the phenomena of *meiosis*, and thus indirectly establishing the significance of the sexual fusion which renders *meiosis* obligatory.

MENDELISM : the modern experimental study of Heredity, based on the work of Gregor Mendel (1822-1869), Praelat of Brnn, who worked on *Pisum sativum* in the monastery garden; paper published 1865, forgotten till 1900. The first to record and interpret observations on the progeny of hybrids of the first generation (F_1), and their successors by interbreeding to F_2 , F_3 , etc.

Experimental Results : Hybrids are not merely mixtures of parental characters, but exhibit *Dominance*; i.e. one character of a complementary pair is normally presented to the exclusion of the other; such a pair is termed an **Allelomorph**; the prevailing character is said to be **Dominant (D)**, and the one masked or really wanting **Recessive (R)**.

The organism is thus conceived as built up of unit-characters as 'factors', which may be isolated for experimental purposes, though any such recognizable character must imply a group of co-ordinated factors, and some may be more readily examined experimentally than others. The 'factor' remains undefined except as it gives experimental results.

Segregation : Numerical results for dominance in succeeding generations were explained by Mendel as suggesting that a gamete carries only one unit of an allelomorphic pair; or, in other words, has the character or has it not. An organism inheriting the same factor from both parents is so far pure for that character, or has a 'double dose' (*homozygote*), and produces gametes all bearing it, of one sort only. An organism inheriting a character from one parent only is *heterozygote*, and produces gametes of two kinds, one with the character and one without, assumed 50 % of each.

Monohybridism. Taking one character only into consideration; if **D** and **R** are parental characters of the σ^7 and q respectively, or *vice versa* (reciprocal cross), the gametes will be all **D** and **R** respectively; the F_1 generation will be **DR**, with the bodily appearance of the **D**.

The gametes of F_1 as parents will be (**D, R**) σ^7 , and (**D, R**) q , giving 4 possible unions for F_2 , as **DD, DR, RD, RR**, in mathematically equal proportions (25 % each) if the law were absolute; i.e. 75 % would carry the dominant character (phenotype), 25 % would be recessive and distinct. Of the phenotype, 25 % would be homozygote (genotype) and equally pure and fixed; but 50 % being still mixtures like the parents (**DR**), would be similarly liable to segregate according to this 1 : 2 : 1 ratio in the F_3 generation. The homozygotes **DD** and **RR**, when interbred among themselves, remain true.

This 'Law of Mendelian Segregation' was deduced by Mendel from his experimental observations. It holds very approximately so long as the factors are reliable; it so far explains the reversion of hybrids to the parent strains, but it makes no advance in making anything new. A mixed strain, self-fertilized, 'Mendelizes out'.

Dihybridism : Of much greater importance is the case of the consideration of two allelomorphs simultaneously, since this gives new combinations, as new strains differing in visible characters, and so far new forms, which may be valuable commercially if they can be maintained pure; i.e. come true to seed.

If **A, B**, are two separate factors, present, their absence may be marked by **a, b**; if one such factor is characteristic of each parent, the original given homozygote parents may be described as **Ab** and **Ba**, either being the σ^7 or q . These would produce gametes as **Ab** and **Ba**, respectively, both σ^7 and q . The F_1 generation will be all of the form **ABab**, in any case, with both dominant characters expressed. But the gametes of this F_1 generation, taking any one expression of both pairs, will be **AB, Ab, aB, ab**, both σ^7 and q . Combination of these in all possible unions gives a schedule of 16 possibilities, included as:—

The Sixteen Square : From this it follows that $\frac{1}{16}$ of the whole F_2 generation will carry the dominant characters of both strains; $\frac{1}{16}$ will be wholly recessive; of the remainder $\frac{1}{8}$ will be dominant to one parental character, and the other $\frac{1}{8}$ to the other parent, and will be readily recognized; or the set will segregate according to a 9 : 3 : 3 : 1 ratio, this being again closely approximated in experimental work, to the extent that if it does not come out it may be fairly assumed that there was something wrong with the 'factors' dealt with, or some other law intervenes.

Also $\frac{1}{16}$ of the whole in each set will be homozygote and so far true, as indicated

in the diagonal series from **AB** to **ab**. All the others will be heterozygote, and will continue to Mendelize out on being interbred to the **F₂** generation, and so on.

In this case since the original parents were homozygote of the type **Ab**, **aB**, two new homozygote combinations appear as new types; e.g. the double dominant and the double recessive: the latter is recognized at once, but half the crop shows double dominant appearance as well as the pure $\frac{1}{16}$: to sort the latter out it will be necessary to grow self-fertilized seed of a number of such plants another season, and select the pure strain which does not break. Assuming tallness as dominant to dwarf habit, and purple pigment dominant to white colour in absence of pigment, the above scheme would illustrate the crossing of a tall white pea with a dwarf red. The same scheme holds for a tall red crossed with a dwarf white; in the latter case the new types would be of the form **Ab** and **aB**.

		♂ AB	Ab	aB	ab
♀	AB	AB AB	Ab AB	aB AB	ab AB
	Ab	AB Ab	Ab Ab	aB Ab	ab Ab
	aB	AB aB	Ab aB	aB aB	ab aB
	ab	AB ab	Ab ab	aB ab	ab ab

Trihybridism, involving working in terms of 3 factors simultaneously, would extend similarly to 64 squares (8 gametes, ♂ and ♀), giving a $27 \cdot 9 \cdot 9 \cdot 9 \cdot 3 \cdot 3 \cdot 3 \cdot 1$ ratio, as 64 types of individual, but in 8 different aspects (phenotypes), and would be correspondingly difficult to handle. But the idea suffices to show the possibilities of increasing complexity, as organisms may be built up of wholly indefinite numbers of factors, and two parents may differ in many characters. In practice it is sufficient to consider one pair (allelomorph, presence or absence of one factor) at a time.

Cytological Interpretation: since Mendelism postulates that every gamete carries one factor only of each pair derived from the parents, and these parental factors are obviously mingled in syngamy, the conclusion appears unavoidable that segregation of factors takes place at the complementary phase of meiosis. The sorting out of P and M chromosomes, in giving the haploid number, is the visible expression of such segregation. In the first meiotic spindle each daughter-nucleus takes either a P or an M chromosome, but not both, for each set of characters the individual chromosomes convey.

This implies that all the factors of an organism are inherited through a mechanism, in which they are divided into as many groups as there are in the haploid number as a specific constant; the possibility of such combinations of P and M chromosomes is considerable, giving a great range of variation in the gametes; this being again increased by the possibilities of fertilization-fusion of any 2 such combinations. The haploid number for Angiosperms ranges from 3 to 45.

Neo-Mendelism introduces indefinite complications; in connexion with:—

(1) Cytology, the chromosomes being regarded as factors (often causal) in the mechanism; cf. 'sex'-chromosome, and number of associated units.

(2) Mutations, since hybridization by affecting the zygote at a crucial period may induce 'sports' or 'mutants'.

(3) The mechanism of segregation being *plasmic* and biological, may go wrong in any respect, at any time.

Hence the 3 component conceptions of Mendelism may fail; e.g.:—

(a) Dominance may be imperfect (case of 'blends' and 'mosaic hybrids').

(β) Segregation may be affected, by influence of factors on one another; as, complementary factors, inhibiting factors, supplementary and cumulative factors, reversion to type, 'crossing over'.

(γ) Unit characters may go wrong, fail, or be lost; non-Mendelian inheritance.

From a comparatively simple new idea the subject rapidly grows in complexity; though undoubtedly the most exciting branch of modern Biology, emphasizing the significance of minute variations in the progeny of the same parents; all such progeny in nature being heterozygote in some respect, however minute. This appears to be the aim of all mechanisms of cross-fertilization, an absolutely pure strain is a fiction of cultivation and autogamy.

General Literature

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 WINKLER (1908), *Berichte*, p. 26, Chimaeras.
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 SCHIMPER (1903, Eng. Trans.) *Plant Geography*; Formations, p. 159; Cold Temperate
 Forest Formations, p. 556.

MINIMUM BOTANY. The preceding schedules, together with a previous issue (*Structural Botany*, Bot. Mem. 4) represent a course of elementary instruction on the botany of Angiosperms, as the higher vegetation of the land surface, adapted for a class of Forestry students, comprising 22 lectures with associated practical work, given in Michaelmas Term (1919) on a revised syllabus. They also cover two-thirds of the general elementary syllabus for the Preliminary Examination in Botany of the School of Natural Science (a set on 'Lower Types' being required to complete the evolutionary scheme).

Experience of the teaching of elementary Botany in the University during the last decades suggests that there is only one aspect of the subject which has proved really of general interest to students and university authorities alike, this being the reduction of such an introductory course to the barest minimum. A fairly reasonable general course formerly taught in two terms (a total of 16 weeks, or 48 lectures), instead of being extended to a full first year's scheme, has been reduced in recent years to a period of 12 weeks, including 36 lectures, to suit the convenience of Medical Students; while an abbreviated course of 8 weeks, or 24 lectures, is now regarded as sufficient for students of Forestry, so far as the general principles of the science are concerned, on the understanding that these students will continue further elementary work in special, 'more useful', branches of the subject. The preceding schedules may be taken as suggestive of the possibilities and limitations of such courses.

That Botany should be described as the most neglected of all modern sciences may be possibly the expression of the incomplete vision of botanists; yet out of a total annual aggregate of about 3,000 students in recent years, not more than 1-3 per cent. (and more often 1 than 3) have attended even elementary botanical courses; the great majority of these again only under the compulsion of an examination-system. The subject is practically ignored by classical and literary circles, and equally so by chemists and physicists; while the elementary course may be said to be merely vestigial in Medicine, as recapitulatory of a phase of Herbalism and Pharmacy. At this time of the world's history it is remarkable that in a university of primary importance, the teaching of Plant-biology should be of such a meagre description.

The fundamental laws of all living organism, including extensions to sociology and theology, are based on biological problems ; and biology, or a knowledge of the laws of life, in some form, should be part of the mental equipment of every educated person. It is again to Botany, as dealing with the primary life of the world—the great independent kingdom of autotrophic vegetation, the base of the pyramid of life, whether in the sea or on the land, and on which we ourselves as animals are still dependent for our supplies of food and energy—that one must look, not only for the interpretation of the primary laws of existence, but also for the broader views rendered possible by the wider range of plant-races, as expressed for example in the elementary mechanism of phyletic progression.

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OXFORD BOTANICAL MEMOIRS

Edited by A. H. CHURCH, M.A.

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